Biomechanical and hydraulic determinants of tree structure in Scots pine: anatomical characteristics

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Summary  The development of anatomical, hydraulic and biomechanical properties in Scots pine (Pinus sylvestris L.) stems aged 7 to 59 years was followed. The hydraulic diameter and length of tracheids increased with age to a maximum at 15 and 35 years, respectively. Number of tracheids per unit of sapwood area decreased with age to a minimum of 500--600 tracheids mm$^{-2}$. Variations in specific hydraulic conductivity and Young’s modulus of stems were associated with variation in anatomical properties.

Over the time sequence considered, hydraulic and mechanical properties were positively related to each other and followed a similar developmental pattern, with no suggestion of a trade-off between the two. For most of the tree’s life-cycle, heartwood made only a small contribution to whole-section mechanical stiffness because of its location close to the flexural neutral axis, and because of the presence of juvenile wood.

Keywords: heartwood, Pinus sylvestris, sapwood, xylem anatomy, xylem conductivity, Young’s modulus.

Introduction

Biomass allocation during tree growth is subject to biophysical constraints. For example, enhanced allocation to foliage increases the photosynthetic productive surface, but also increases requirements for mechanical support and water and nutrient uptake. Trees achieve massive size through allocation to wood, which has three main functions: (i) mechanical support, (ii) water, carbon and nutrient transport, and (iii) storage.

Evidence for the relative importance of these functions is contradictory. Historically, hydraulic needs have received considerable attention (Jarvis 1975, Waring et al. 1977, Zimmermann 1983, Tyree and Ewers 1991), but our knowledge of biomechanical constraints is now quickly expanding (McMahon and Kronauer 1976, King 1981, Morgan and Cannell 1987, Niklas 1992, Coutts and Grace 1995). Because theoretically optimal allocation strategies are not easily identified, measured patterns are seldom compared with null hypotheses of biomass allocation (Farnsworth and Niklas 1995); likewise, comparisons of xylem relative efficiency for hydraulic versus mechanical function are infrequent (Gartner 1991a, 1991b, 1991c).

Biomass allocated to xylem production can give rise to a relatively large cross-sectional area of low density wood or a smaller cross-sectional area of higher density wood (i.e., there is a trade-off between tracheid or vessel lumen diameter and wall thickness). Either pattern of development can meet the hydraulic and mechanical requirements of the tree, depending on the particular distribution of dry matter at the anatomical scale (Schniewind 1962).

Sapflow is largely restricted to the outer portion of a stem cross section (i.e., the sapwood), whereas mechanical support is provided by both sapwood and heartwood. Thus, the distribution of the hydraulic and biomechanical functions between sapwood and heartwood influences sapwood maintenance cost.

Here we report an investigation of interactions between hydraulic and mechanical properties of stems during tree development. We first describe relationships between anatomical characteristics, and hydraulic and biomechanical properties for Scots pines ranging in age from 7 to 59 years. We then estimate the respective roles of sapwood and heartwood for the mechanical support of the crown.

Materials and methods

Site description

The site was an extensive plantation of Scots pine (Pinus sylvestris L.) and Corsican pine (Pinus nigra var. maritima (Ait.) Melv.) in Thetford Forest, East Anglia, U.K. Climatic data for the forest have already been presented (Mencuccini and Grace 1995). Average summer precipitation is 170 mm and average July temperature is 17.0 °C. Soil characteristics are given by Corbett (1973).
Ten areas were selected in even-aged stands of Scots pine, with tree age (measured from the year of planting) ranging from 7 to 59 years (Table 1). Genetic variability among stands was standardized by using Forestry Commission archives to select the stands on the basis of age and origin. Eight stands were derived from seed collected from local seed orchards. The two youngest stands were naturally regenerated from nearby seed sources.

**Sampling strategy**

For each site, we selected two 20-m-diameter plots in the 7-, 14- and 18-year-old stands and two 40-m-diameter plots in the older stands. The stem diameters at 1.3 m from the ground were measured to the nearest cm. Within each site, three dominant trees (total of 30) were selected and cut for intensive sampling during late September 1993. For each tree, samples were taken to determine xylem anatomical properties, stem specific conductivity, and Young’s modulus of elasticity.

**Xylem specific conductivity**

For every sample tree, two stem disks were taken for measurement of xylem specific conductivity. The disks were cut below the live crown base and at the base of the upper third of the crown. Each stem disk was subsampled by cutting specimens in various positions within the section. Sapwood and heartwood were sampled separately. Sapwood was produced at the cut ends. The next day cut surfaces were chiseled with a sharp planer angled at about 30°. This method proved most effective in eliminating resin and sawdust residues from the cut surfaces (cf. Booker 1984).

Inlet and outlet pipes were connected to the cut faces of stem sections, and a constant head of distilled, filtered (to 0.2 µm) water was used to apply a known pressure (∆P, MPa) gradient. The volumetric outflow (q, m³ s⁻¹) was collected on a balance. Specific conductivity was calculated according to Darcy’s law (Siau 1984):

\[
k_{s,m} = \frac{q l}{A_s ∆P},
\]

where \(k_{s,m}\) is measured wood specific conductivity or permeability (m²); \(A_s\), \(l\), and \(η\) are conductive sapwood area (m²), sample length (m), and dynamic water viscosity (MPa s), respectively. In total, 60 samples were measured.

**Young’s modulus**

After measurement of specific conductivity, stem disks were kept water saturated in plastic bags in a refrigerated room for a maximum of two weeks. Samples were measured for Young’s modulus of elasticity and anatomical characteristics. Only disks from the living crown base were selected for anatomical measurements.

Mechanical measurements were made on all disks from the base of the living crown and on selected samples from the upper third of the crown. Each stem disk was subsampled by cutting specimens in various positions within the section. Sapwood and heartwood were sampled separately. Sapwood was further divided into four concentric portions sampled at three radial positions 120° apart, giving a total of 12–15 specimens per stem disk. The specimens, which were cut along the grain, had a cross section of 20 × 10 mm and a length of about 20 cm. After preparation for the mechanical test, specimens were stored in plastic bags to protect them from dehydration.

The apparent Young’s modulus of wood (\(E_{app}\), N m⁻²) was measured at room temperature (~20 °C) on a standard engineering rig (Instron Universal Testing Instruments, Model TT-D, Canton, MA), using a one-point loading test (Cannell and Morgan 1987). The sections were bent on the tangential surface as simple beams supported at each end, with loads and deflections being measured at the midpoints of the sections.

<table>
<thead>
<tr>
<th>Site</th>
<th>Stand code</th>
<th>Age (year)</th>
<th>No. of trees ha⁻¹</th>
<th>Basal area (m² ha⁻¹)</th>
<th>D (cm)</th>
<th>H (m)</th>
<th>Height of crown base (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lynford</td>
<td>4087</td>
<td>7</td>
<td>3280</td>
<td>7.01</td>
<td>6.8</td>
<td>1.6</td>
<td>0.22 (0.7)</td>
</tr>
<tr>
<td>Hockham</td>
<td>9036</td>
<td>7</td>
<td>3285</td>
<td>7.03</td>
<td>6.9</td>
<td>2.2</td>
<td>0.37 (1.4)</td>
</tr>
<tr>
<td>Santon</td>
<td>5016</td>
<td>14</td>
<td>3133</td>
<td>40.34</td>
<td>12.8</td>
<td>7.7</td>
<td>1.68 (0.4)</td>
</tr>
<tr>
<td>Lynford</td>
<td>4086</td>
<td>18</td>
<td>3883</td>
<td>30.48</td>
<td>10.0</td>
<td>9.9</td>
<td>1.55 (0.2)</td>
</tr>
<tr>
<td>Lynford</td>
<td>4078</td>
<td>32</td>
<td>1560</td>
<td>48.63</td>
<td>19.9</td>
<td>16.9</td>
<td>7.86 (1.6)</td>
</tr>
<tr>
<td>Santon</td>
<td>3047</td>
<td>33</td>
<td>1783</td>
<td>48.58</td>
<td>18.6</td>
<td>18.4</td>
<td>11.9 (2.2)</td>
</tr>
<tr>
<td>Harling</td>
<td>8029</td>
<td>43</td>
<td>796</td>
<td>41.12</td>
<td>25.6</td>
<td>19.5</td>
<td>11.9 (1.5)</td>
</tr>
<tr>
<td>Hockham</td>
<td>9047</td>
<td>46</td>
<td>732</td>
<td>38.32</td>
<td>25.8</td>
<td>19.1</td>
<td>11.3 (1.0)</td>
</tr>
<tr>
<td>Croxton</td>
<td>5036</td>
<td>58</td>
<td>430</td>
<td>34.95</td>
<td>32.2</td>
<td>24.2</td>
<td>14.8 (0.1)</td>
</tr>
<tr>
<td>Harling</td>
<td>8033</td>
<td>59</td>
<td>398</td>
<td>38.05</td>
<td>34.8</td>
<td>21.7</td>
<td>13.4 (0.2)</td>
</tr>
</tbody>
</table>

1 Age is calculated from date of planting. Values for number of trees ha⁻¹, stem basal area (at 1.3 m) ha⁻¹, and stem diameter at breast height (D) (base of crown for the saplings) are the mean for two 40-m-diameter plots (20-m-diameter plots in the four youngest stands) established in each stand before sample trees were felled. Symbol H denotes the average height of the three sampled dominant trees per stand. Numbers in parentheses are standard deviations.
using load cells and linear transducers output to chart recorders. Because the deflections measured in this way include a component due to shear forces, the true modulus of elasticity ($E$, N m$^{-2}$) was derived from $E_{\text{app}}$, assuming $E/G = 45$, where $G$ is the modulus of rigidity (see the Appendix of Cannell and Morgan (1987) on the theory for calculating $E$, when $E/G$ is known). The value of $E/G$ was obtained from Brown (1989) for living branches and stems of Pinus contorta Doug. ex Loud. The span (i.e., distance between supports) was 15 cm and the average ratio of span to width, $L/d$, was 15 (British Standards Institution 1979, American Society for Testing and Materials 1980). This considerably reduced the magnitude of the correction due to shear forces, which varied between 18 and 27%.

Specimens were loaded at a constant rate of 0.5 mm min$^{-1}$. Apparent modulus of elasticity of wood ($E_{\text{app}}$) was calculated from the linear regions of the load-deflection (stress--strain) curve.

After the mechanical measurements, wood basic density ($\rho_w$) was determined for each specimen. A measure of density-specific stiffness was then obtained as:

$$ \text{Density-specific stiffness} = \frac{E}{\rho_w}, \quad (2) $$

Because $E$ increases nonlinearly with wood density (see Results), the ratio indicates the extent to which a plant stem increases its material stiffness relative to its mass (i.e., self-loading) (Niklas 1993).

The Young’s modulus of whole sections, $\bar{E}$ (GN m$^{-2}$), was estimated from the measurements of individual specimens as:

$$ \bar{E} = \frac{E_h I_h + E_i I_i + E_m I_m + E_s I_s}{I_{\text{tot}}}, \quad (3) $$

where $E_h$, $E_i$, $E_m$ and $E_s$ are the average Young’s modulus for heartwood, inner, middle and outer sapwood, respectively, and $I_h$, $I_i$, $I_m$, and $I_s$ are the corresponding second moment of area (Niklas 1992); $I_{\text{tot}}$ is the second moment of area for the whole section, calculated as:

$$ I_{\text{tot}} = \frac{\pi r^4}{4}, \quad (4) $$

where $r$ is the disk radius. Flexural stiffness, $E_{\text{tot}}$, represents the bending moment required to bend a beam to a certain curvature (Niklas 1992).

**Xylem anatomical measurements**

Wood basic density $\rho_w$ (kg m$^{-3}$) was calculated as:

$$ \rho_w = \frac{W_d}{V_t}, \quad (5) $$

where $W_d$ and $V_t$ are dry mass (kg) and fresh volume (m$^3$) of the sample, respectively. Wood fresh volume was measured by means of a water displacement method.

Because $E$ depends on water content, ($C_{\text{w}}$) (Carrington 1922), parallel experiments were run by dehydrating 10 specimens on the bench and periodically monitoring their $E$, to determine the relationship between $E$ and $C_{\text{w}}$ in our samples.

**Tracheid number and lumen diameter**

From the same portions of stem disks used for mechanical sampling, the outermost four to five rings were sampled for anatomical measurements. Two transverse sections of 40 $\mu$m were cut from each stem disk, stained with safranin and embedded in glycerine. A system utilizing a microscope, a computer and image analysis software was used to estimate for each image field: (a) tracheid lumen diameters; (b) number of tracheids per unit area; and (c) percentage of area occupied by tracheid lumina. Image fields were chosen in the first few rows of each earlywood ring to avoid effects of reduction on tracheid diameters with position inside the ring. Two fields were measured for each of four to five rings, for a total of about 200 tracheids per field and 1,600–2,000 tracheids per stem disk.

The software automatically measured the two axes of each tracheid, i.e., maximum width and the length of the segment perpendicular to the axis of maximum width. Tracheids were approximately rectangular in shape. The two axes were used to calculate the short and long sides of the rectangle, and the tracheid hydraulic diameter, $d_h$, i.e., diameter of the capillary of circular cross section having the same flow rate under the same pressure gradient (Nonweiler 1975, Zimmermann and Jeje 1981). For rectangles, hydraulic diameter equals (Lewis 1992):

$$ d_h = \frac{2ab}{a + b}, \quad (6) $$

where $a$ and $b$ are the two sides.

Weighted averages of hydraulic diameters for each section were calculated using the formula (Sperry et al. 1994):

$$ \bar{d}_h = \frac{\sum d_h^i}{\Sigma d_i}, \quad (7) $$

which weights hydraulic diameters of single tracheids according to hydraulic conductance (assumed proportional to $d_h^4$).

Theoretical specific conductivity of each disk was calculated according to the equation for capillaries:

$$ k_{\text{theor}} = \frac{\pi}{128} \sum_{i=1}^{n} d_{h,i}^4, \quad (8) $$

where $k_{\text{theor}}$ is theoretical wood specific conductivity (m$^2$), $d_{h,i}$ are hydraulic diameters of single tracheids and the summation is over number of tracheids, $n$, per unit cross-sectional area.

**Tracheid length**

Another subsample adjacent to the previous one was used to estimate tracheid length. Earlywood of the five outermost rings was separated from the latewood (Jingxing 1989) and macerated in a solution of acetic acid and hydrogen peroxide at 50 °C.
for about 2 h. The tracheids were then washed and stained in a solution of methylene blue and glycerine gel. Randomly selected tracheids were mounted on a slide and the lengths of about 100 tracheids per sample were measured.

Statistical analyses

Changes in wood anatomical, hydraulic and mechanical properties as a function of tree age for 30 sample trees were analyzed by nonlinear regression methods based on the Marquardt algorithm. After preliminary analysis, the following model gave a good fit to the data:

\[ y = \alpha - \beta e^{-\gamma t}, \]  

(9)

where \( y \) is wood property developing through time \( t \) (in years) and \( \alpha, \beta \) and \( \gamma \) are the estimated asymptotic maximum value of \( y \), the difference between the maximum and the minimum (extrapolated at year 0) and the time constant for the 95% change in \( y \), respectively.

The 30 sample trees were grouped into five age classes (approximately 7, 15, 30, 45 and 60 years). Differences in anatomical, hydraulic and mechanical properties among tree age classes were analyzed by one-way ANOVA; multiple comparisons were made by orthogonal polynomial contrast tests (Steel and Torrie 1980). Anatomical, hydraulic and mechanical properties were also related to each other using similar nonlinear regression models.

Results

Anatomical properties

The weighted hydraulic diameter (\( \bar{d}_h \)) of tracheid lumens (Equation 8) significantly increased from the first (25 \( \mu \)) to the second tree age class (35 \( \mu \)) and then remained substantially constant in the other four age classes (Table 2). The unweighted mean hydraulic diameter followed a similar trend, but with 30–40% lower values. The parameters predicted by nonlinear regression using the model represented by Equation 9 are given in Table 3.

Tracheid length increased more gradually with tree age (Table 2), from about 1.0 mm at 7 years to about 2.6 mm at 45 years, thus the predicted time constant was larger than that for tracheid diameter (Table 3).

Wood basic density varied among age classes (Table 2), with the last two classes having significantly greater values (\( F = 28.4, P < 0.00001 \)).

Hydraulic properties

Specific conductivity, \( k_s \), increased consistently with tree age, from about 1.2 \( \times 10^{-12} \) \( \text{m}^2 \) at 7 years to an asymptote of about 4.0 \( \times 10^{-12} \) \( \text{m}^2 \) (Table 4). At the base of the crown, the equation predicted a 95% change in 26 years (Table 3). A similar trend can be observed at the base of the upper third of the crown. For each tree, values at the base of the living crown were generally larger than inside the crown.

Stem \( k_s \) was significantly related both to tracheid \( d_h \) and \( l \) (Table 5), and the best equation for the prediction of \( k_s \) included both independent variables:

\[ k_s = 0.1768 \times 10^{-12} (l/d_h)^{0.699} \]  

\( R^2 = 0.68 \)

Measured values of \( k_s \) were significantly related to the calculated theoretical values based on Equation 7 (\( R^2 = 0.55, P < 0.00001 \)) but were on average only about 40% (± 2%) of the theoretical values.

Biomechanical properties

Dehydration experiments (\( n = 10 \)) showed that specimen \( E \) did not change for values of \( C_w \) greater than 30%. Below 30%, an increase in \( E \) was evident. For the present analysis, we excluded all samples having a \( C_w \) value below 50% (final sample size \( n = 296 \)).

Young’s modulus of elasticity for a single specimen’s \( E \) was related to cambial age (\( A_c \)) (Figure 1), tree age (\( A_t \)) (or any other measure of tree size):

\[ \ln E = 0.3204 + 0.4205 \ln A_c, \]  

\( R^2 = 0.44 \)  

\( P < 0.0001 \)

and wood basic density, \( \rho_w \):

\[ \ln E = 3.2758 + 1.5506 \ln \rho_w, \]  

\( R^2 = 0.22 \)  

\( P < 0.0001 \).

The slope of the relationship with wood basic density was significantly larger than one (\( P < 0.001 \)), indicating that with a unit increase in density there was a proportionately larger increase in \( E \).

Density-specific stiffness \( E/\rho \) was associated with the same variables used for \( E \) and was also strongly linked to \( E \) (Figure 2):

\[ \log E/\rho_w = 1.2095 + 0.8572 \log E \]  

\( R^2 = 0.91 \)  

\( P < 0.00001 \),

with the slope of the relationship being significantly smaller than one (\( P < 0.001 \)).

Young’s modulus for whole sections increased with tree age from about 1.7 GN \( m^{-2} \) at 7 years to about 7.9 GN \( m^{-2} \) at 25 years and then remained substantially constant (Table 4). The same pattern was evident also for \( E/\rho_w \) (\( R^2 = 0.81, \) ratio = 342.0).

Whole-section \( \bar{E} \) was positively related to earlywood tracheid \( l \), earlywood tracheid \( d_h \), and to an area-weighted measurement of wood basic density for whole sections (Table 5).

Whole-section \( E \) was also positively related to specific conductivity (Figure 3) and increased with tree age at a similar rate (i.e., time constant).

Young’s modulus \( E \), second moment of area \( I \), and flexural stiffness \( EI \) were also strictly related to disk diameter (\( R^2 \) between 0.784 and 0.997).
Table 2. Anatomical properties (± SE) in Scots pine trees of different ages.1

<table>
<thead>
<tr>
<th>Tree age class</th>
<th>Unweighted hydraulic diameter (µm)</th>
<th>Weighted hydraulic diameter (µm)</th>
<th>Tracheid length (mm)</th>
<th>Tracheids per mm²</th>
<th>Area in tracheids (%)</th>
<th>Wood basic density (kg m⁻³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>18.91 ± 0.63 a</td>
<td>23.78 ± 0.47 a</td>
<td>1.00 ± 0.05 a</td>
<td>918 ± 32 a</td>
<td>53.3 ± 2.2 a</td>
<td>0.367 ± 0.01 a</td>
</tr>
<tr>
<td>15</td>
<td>27.66 ± 0.52 b</td>
<td>36.17 ± 1.04 b</td>
<td>1.81 ± 0.08 b</td>
<td>656 ± 27 b</td>
<td>68.0 ± 2.8 b</td>
<td>0.369 ± 0.01 a</td>
</tr>
<tr>
<td>30</td>
<td>26.51 ± 0.84 b</td>
<td>34.51 ± 1.16 b</td>
<td>2.37 ± 0.05 c</td>
<td>593 ± 29 b</td>
<td>60.6 ± 0.7 ab</td>
<td>0.373 ± 0.01 ab</td>
</tr>
<tr>
<td>45</td>
<td>25.07 ± 0.53 b</td>
<td>33.62 ± 0.91 b</td>
<td>2.59 ± 0.08 c</td>
<td>556 ± 35 b</td>
<td>54.9 ± 1.3 a</td>
<td>0.425 ± 0.01 bc</td>
</tr>
<tr>
<td>60</td>
<td>26.90 ± 0.57 b</td>
<td>34.22 ± 1.22 b</td>
<td>2.55 ± 0.03 c</td>
<td>545 ± 36 b</td>
<td>58.7 ± 1.4 a</td>
<td>0.461 ± 0.02 c</td>
</tr>
</tbody>
</table>

1 Values are means for the 30 sample trees grouped into five approximate age classes (see statistical analysis). Results were evaluated by ANOVA; comparisons among age classes were made with an orthogonal polynomial contrast test ($n = 5$). Different letters in a column indicate significant differences at $P < 0.01$. Theoretical specific conductivity $\kappa_\text{ref}$, varied with sampling position. Within each tree, values for stems inside the crown were generally lower than at the crown base, but even-

Table 4. Hydraulic and mechanical properties (± SE) in Scots pine trees of different ages.1

<table>
<thead>
<tr>
<th>Tree age class</th>
<th>BLC</th>
<th>UC</th>
<th>Theoretical specific conductivity (GN m⁻²)</th>
<th>Young’s modulus (GN m⁻²)</th>
<th>Second moment of area $I_{\text{tot}}$ (10⁸ m⁴)</th>
<th>Flexural stiffness $E I_{\text{tot}}$ (10⁷ m⁻² GN)</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>1.25 ± 0.20 a</td>
<td>1.90 ± 0.23 a</td>
<td>3.40 ± 0.36 a</td>
<td>1.71 ± 0.17 a</td>
<td>0.023 ± 0.00 a</td>
<td>0.0004 ± 0.00 a</td>
</tr>
<tr>
<td>15</td>
<td>2.83 ± 0.15 b</td>
<td>2.46 ± 0.26 ab</td>
<td>11.60 ± 0.88 b</td>
<td>5.72 ± 0.40 b</td>
<td>2.19 ± 0.32 ab</td>
<td>1.22 ± 0.16 ab</td>
</tr>
<tr>
<td>30</td>
<td>3.41 ± 0.25 bc</td>
<td>2.71 ± 0.12 b</td>
<td>8.76 ± 0.78 c</td>
<td>7.91 ± 0.42 c</td>
<td>4.31 ± 1.84 ab</td>
<td>3.13 ± 1.19 ab</td>
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<tr>
<td>45</td>
<td>3.46 ± 0.27 bc</td>
<td>3.11 ± 0.14 bc</td>
<td>6.67 ± 0.23 c</td>
<td>7.40 ± 0.47 c</td>
<td>5.63 ± 0.16 bc</td>
<td>3.99 ± 0.64 bc</td>
</tr>
<tr>
<td>60</td>
<td>3.80 ± 0.14 c</td>
<td>3.71 ± 0.11 c</td>
<td>8.23 ± 0.32 c</td>
<td>7.89 ± 0.41 c</td>
<td>9.05 ± 1.28 c</td>
<td>7.13 ± 1.09 c</td>
</tr>
</tbody>
</table>

1 Values are means for the 30 sample trees grouped into five approximate age classes (see statistical analysis). Results were evaluated by ANOVA; comparisons among age classes were made with an orthogonal polynomial contrast test ($n = 5$). Different letters in a column indicate significant differences at $P < 0.01$. Symbols: BLC is the base of living crown, and UC is the base of upper third of crown. Theoretical specific conductivity was calculated according to Equation 8.

Discussion

General trends in wood anatomical, hydraulic and mechanical properties

Trends shown in this paper are similar to those of other studies relating anatomical features to either mechanical or hydraulic parameters. However, few studies have considered these three sets of properties together (e.g., Gartner 1991a, 1991b).

Wood specific conductivity was significantly related to tracheid length and diameter. These correlations may reflect real mechanistic relationships governing patterns of water movement in single tracheids. Viscous resistances to water flow are located both in the vessel lumen and in the bordered pits, probably as resistances of the pores in the pit membrane itself (Bolton 1976, Bolton and Petty 1978). It is likely, therefore, that tracheid length is related to water flow resistance by defining the number of times water must pass through a bordered pit, and thus by correlation between length and number of bordered pits (Pothier et al. 1989, Jingxing 1989).

Values of wood specific conductivity, $\kappa_\text{ref}$, varied with sampling position. Within each tree, values for stems inside the crown were generally lower than at the crown base, but even-
tually reached a similar asymptotic value. Values were also similar for saplings. Patterns of $k_s$ at different crown positions are likely to reflect differences in the degree of cambial cell maturation (expressed as number of rings from pith).

Mechanistic physiological bases for the understanding of variability in Young’s modulus of elasticity, $E$, are not completely satisfactory. Traditionally, $E$ has been related, for practical purposes, to a bulk measure of wood density and to the
percent of latewood (e.g., Bodig and Goodman 1973, Kollmann and Côté 1984, Pearson and Ross 1984). However, $E$ can be increased also by a reduction in the inclination angle of microfibrils, which is a common phenomenon during tree growth (Bendtsen and Senft 1986, Schniewind and Gammon 1986). Therefore, it is not surprising that the increase in wood density observed during development brought about a more than proportional increase in $E$ (Bendtsen and Senft 1986). The cumulative effects of these different anatomical properties on $E$ are also confirmed by the large increase in $E/\rho_w$ with $E$, indicating that other variables beside wood density have changed (Wilson and White 1986, Gartner 1995).

Variation in density specific stiffness with tree age are seldom considered in biomechanical analyses. Based on Euler’s buckling formula, the critical height $H_{\text{crit}}$ that a vertical tree trunk can reach before it undergoes elastic buckling is given by the formula:

$$H_{\text{crit}} = C\left(\overline{E}/\rho_w\right)^{1/3}D^{5/3},$$

where $C$ is a constant of proportionality and $D$ is stem diameter. This equation has been widely used for predicting the safety factors for height growth based on engineering principles, on the assumption that density specific stiffness does not scale with diameter. In our data set, $E/\rho_w$ does scale with stem diameter as: $E/\rho_w \propto D^{1.11}$ (calculated with reduced major axis regression), or as: $E/\rho_w \propto D^{0.94}$ (calculated by least square regression) with the two values being close to one. As predicted, it was found (unpublished results) that the exponent of the relationship between diameter and height in our age sequence is significantly larger than $\alpha = 2/3$.

### Relationships between hydraulic and mechanical properties

A significant positive relation between $k_s$ and $\overline{E}$ was found and the time constants for the 95% change as estimated by nonlinear regression were similar (Table 3). Increases in $k_s$ and $E$ are advantageous because an increase in height during growth influences both the distance water must travel from the soil to the transpiring leaves, and the magnitude of the bending moment under conditions of dynamic wind loading.

During growth, Scots pine trees seem able to accommodate both changes by simultaneously altering the relevant anatomical properties. To some extent, therefore, no simple trade-off was evident at the anatomical scale. However, it has been shown that when “viney” poison oak plants were grown without an external support, they produced denser wood with higher material stiffness and lower specific conductivity (Gartner 1991a, 1991b). It could be argued, therefore, that because the mechanical support function needs to be simultaneously optimized, water-conducting elements cannot be as large as they would otherwise be (Gartner 1991c, Farnsworth and Niklas 1995).

Both $k_s$ and $\overline{E}$ showed a linear increase during the first few years of xylem development, followed by a nonproportional increase and eventually a plateau. Thus, a relevant question is whether this final stage of wood development has any biologi-

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**Table 5. Matrix of correlation coefficients for the relations between anatomical, hydraulic and mechanical properties in Scots pine.**

<table>
<thead>
<tr>
<th>$\overline{d}_h$</th>
<th>$l$</th>
<th>$\rho_w$</th>
<th>$k_\text{theor}$</th>
<th>$k_\text{m}$</th>
<th>$\overline{E}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\overline{d}_h$</td>
<td>1</td>
<td>0.81</td>
<td>0.24 ns</td>
<td>0.93</td>
<td>0.77</td>
</tr>
<tr>
<td>$l$</td>
<td>1</td>
<td>0.50</td>
<td>0.71</td>
<td>0.88</td>
<td>0.73</td>
</tr>
<tr>
<td>$\rho_w$</td>
<td>1</td>
<td>0.06 ns</td>
<td>0.33 ns</td>
<td>0.45*</td>
<td></td>
</tr>
<tr>
<td>$k_\text{theor}$</td>
<td>1</td>
<td>0.75</td>
<td>0.74</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$k_\text{m}$</td>
<td>1</td>
<td>0.85</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\overline{E}$</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Symbols: $\overline{d}_h$, weighted tracheid hydraulic diameter (Equation 8, $\mu$m); $l$, tracheid length (mm); $\rho_w$, wood basic density (kg m$^{-3}$); $k_\text{theor}$, theoretical specific conductivity (Equation 9, m$^{-3}$); $k_\text{m}$, measured specific conductivity at the base of the living crown (m$^{-3}$); $\overline{E}$, Young’s modulus of elasticity (GN m$^{-2}$). All coefficients significant at $P < 0.01$, unless indicated; ns, not significant ($P > 0.05$); *, significant at $P < 0.05$. Variables were log-transformed.
tical meaning. Theoretically, higher values of $k$ and $E$ can be obtained simultaneously by changing earlywood vessel diameter and pit pore size, latewood density and fibril angle. It is possible that trade-offs involve additional properties besides the two measured ones, e.g., vulnerability to cavitation of the water transport system and other mechanical properties relevant for tree stability (e.g., strength or torsional rigidity, Vogel 1995).

For instance, Hargrave et al. (1994) showed that large and long vessels inside individuals of *Salvia mellifera* Greene were more prone to cavitation, because of both the larger size of membrane pores and the enhanced probability of having larger pores in the numerous pits of long vessels.

**Relative importance of sapwood and heartwood for mechanical support during tree growth**

During tree growth, inner dysfunctional rings are gradually transformed to heartwood. It is not completely clear what mechanisms control heartwood formation, but they have been shown to be linked with the processes of pit membrane degradation and embolism development in *Populus tremuloides* Michx. (Sperry et al. 1991). At the tree scale, number of sapwood rings was shown to be strongly related to tree age, irrespective of density and fertility conditions (Coyea et al. 1990), suggesting that developmental events are associated with this transition. Heartwood is often considered to have a mechanical support function; however, direct evidence for the existence of such a function is lacking (Gartner 1995).

We estimated the relative contributions of heartwood and sapwood to total section flexural stiffness, using the approach in Equation 3 and the measured values of Young’s modulus. Growth for a hypothetical Scots pine tree stem at 1.3 m from the ground was simulated over time and the mechanical properties for each individual ring estimated using the following measured relations (a), (b) and (c) and assumption (d): (a) stem radial increment increases with age, peaks at 15 years and then declines to a constant value (Mencuccini and Grace 1995, and unpublished data); (b) Young’s modulus varies with cambial age (i.e., number of rings from pith) as shown in Figure 1; (c) number of rings in sapwood increases asymptotically with age up to a constant value for old trees (unpublished data, cf. Coyea and Margolis 1994); (d) each ring is either entirely sapwood or entirely heartwood. We then estimated flexural stiffness for each ring and partitioned flexural stiffness of the whole section (calculated according to Equation 3) by grouping rings into heartwood and sapwood. The simulation was extended beyond the analyzed range simply to illustrate the expected hypothetical development.

In general, heartwood contributed less than 50% to whole-section flexural stiffness (Figure 8, open squares). Only in very old trees, where radial growth was slight and heartwood accounted for more than 80% of total diameter, did heartwood contribute more than 50%. This low contribution of heartwood may be due to its location close to the flexural neutral axis, and to the fact that heartwood is mostly made up of juvenile wood with lower elastic properties.

It appears, therefore, at least in Scots pine, which maintains a large number of sapwood rings, that sapwood provides: (1) storage of water, nutrients and carbohydrates, (2) the hydraulic supply to the crown, and (3) most of the mechanical support required by the tree.

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**References**


